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Primary Productivity in a Nutrient-Limited Tropical Estuary[1]

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ABSTRACT: The results of a survey of phytoplankton productivity, chlorophyll a and nutrient concentrations in Pala Lagoon, American Samoa, are shown to be interpretable in terms of two regimes: an ocean-dominated region where productivity is controlled by fixed nitrogen concentrations, and a land-runoff-dominated regime where productivity is unrelated to major nutrient concentration. A quantitative relationship between nutrient concentrations in the lagoon and phytoplankton growth rates is presented. This relationship is used as the basis for predicting the effects of a proposed dredging operation within the lagoon as well as for predicting the effects of increased waste discharge into the local marine environment.

PALA LAGOON, on the southern coast of Tutuila Island, American Samoa, is a tropical estuary roughly circular in shape of about 1 mile diameter with an entrance channel at the southern end aligned eastward (Fig. 1). The mean depth is about 1.5 meters although much deeper dredged holes exist in and near the entrance channel. The lagoon is moderately turbid, and receives a large amount of seasonal stream runoff, mostly during the period December to March. The annual rainfall is about 130 inches and a considerable portion of the bottom is covered with a layer of silty mud.

Sewage treatment is nonexistent for the communities bordering the lagoon, wastes being discharged into the lagoon via the many streams originating in the volcanic mountain range running the length of the island.

To improve the economic and recreational value of the lagoon, it has been proposed that rather extensive dredging operations be conducted for the channel and adjacent areas; and construction of a small boat harbor is anticipated. The present study is part of an overall reconnaissance being made by scientists from the University of Hawaii in cooperation with the government of American Samoa to determine the advisability of further altering circulation patterns inside the lagoon. Reported here are the results of a week-long survey in March 1972 of phytoplankton biomass and productivity and associated macronutrient concentrations.

METHODS

To establish station locations for more detailed study, we made an initial reconnaissance of the plant pigment concentrations in Pala Lagoon using *in vivo* fluorometry (Lorenzen, 1966). A shallow draft outboard motorboat was outfitted with a portable generator, pump, and fluorometer (Turner model III with continuous-flow door and Rustrak recorder). While the lagoon was being circumnavigated, water was being pumped continuously from a depth of about 0.5 meter through an opaque length of garden hose. The data we obtained, presented in Fig. 1, made possible the establishment of a series of representative station locations within the lagoon. On the following 2 days, working from a smaller rubber boat, we collected discrete surface water samples from each of these stations. The following procedures were employed to collect and analyze these samples: productivity samples were taken in standard glass BOD bottles (two light, one dark) which were stored in the dark for not more than 45 minutes until they could be inoculated. Samples for nutrient analyses were taken in polyethylene bottles and stored in an ice chest containing Dry Ice. Additional fluorometry samples were also collected at each station.

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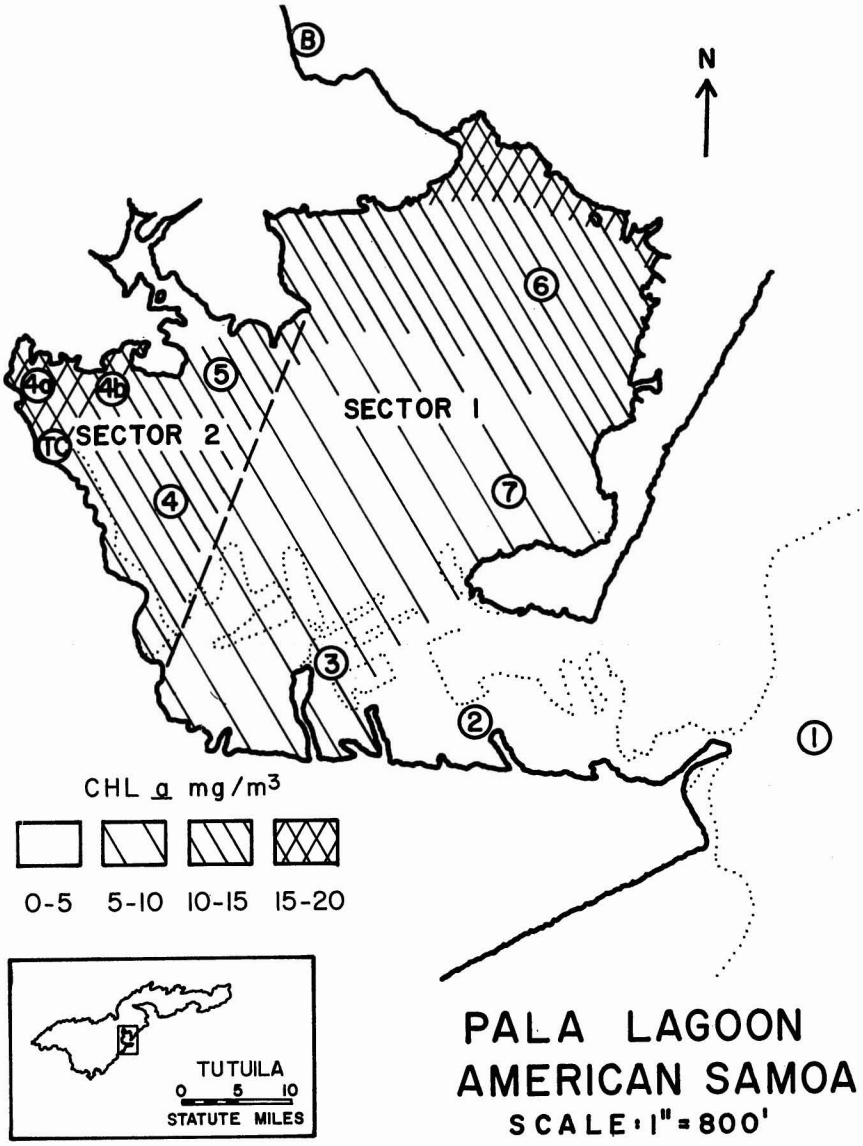

FIG. 1. Chlorophyll a concentrations during the preliminary fluorometric survey and subsequent station locations. The dashed line represents the approximate interface between the two sectors.

Primary productivity was determined by the C^{14} method of Steeman-Nielsen (1952) as modified by Strickland and Parsons (1968). Upon returning to shore (near station 2), we inoculated samples with 1.0 μCi of $NaH^{14}CO_3$ in 1.0 ml of sterile water at pH 9.5 (New England Nuclear) and incubated them in about 1 meter of water for about 4 hours between the hours of 1100 and 1700. Samples were then filtered through 0.45-μ Millipore filters, rinsed, glued to copper planchettes, and stored in a desiccator. Upon returning to Hawaii, we counted the filters in a gas-flow Geiger counter (Nuclear Chicago model 1042 with an end window) which was calibrated by liquid scintillation (Wolfe and Schelske, 1967).

TABLE 1

Summary of Data from All Stations

Station	Date	Salinity (0/00)	Temperature (° C)	Nutrient concentrations (μg-at/liter): Nitrate and nitrite—N	Ammonia—N	Phosphate—P	Chlorophyll a (mg m^{-3})	Productivity (mg C fixed/ m^{-3} hr^{-1})	Productivity index (mg C fixed)/ (mg chl a-hr)
1	2/29	33.9	30	0.63	0.93	0.14	0.55	8.32	15.13
2	2/29	33.0	30	0.19	0.07	0.13	4.18	38.17	9.13
3	2/29	32.0	32	0.00	0.03	0.15	6.94	49.76	7.17
4	2/29	32.0	33	0.53	0.10	0.13	11.01	65.80	5.98
4*a*	3/1	28.2	32.5	1.47	0.12	0.33	17.87	145.17	8.12
4*b*	3/1	30.1	32	—	—	—	11.36	—	—
5	3/1	31.0	32	0.75	0*	0.28	11.36	63.00	5.55
6	3/1	32.0	32	0.05	0.02	0.14	12.79	45.96	3.59
7	3/1	32.3	32	0.00	0*	0.09	5.97	38.60	6.47
B	3/2	0.0	—	0.74	0*	2.00	1.52	—	—
TC	3/2	24.2	32	2.90	0.34	0.41	11.45	—	—
A1	3/2	27.9	33	2.15	0.98	0.13	2.06	8.28	4.03
A2	3/2	31.5	35	0.00	0.03	0.18	28.40	86.10	3.03

Note: dash indicates that no analysis was made.
* Reagent blank exceeded sample value.

Nutrient samples were kept frozen until the return to Hawaii. Reactive nitrate (plus nitrite) -nitrogen and reactive phosphate-phosphorous determinations were made by the methods outlined in Strickland and Parsons (1968). Ammonia was determined by the method of Solorzano (1969).

We determined chlorophyll a from total plant pigment concentration by using a conversion factor calculated for the fluorometer used (S. A. Cattell, personal communication).

Nutrient analysis and chlorophyll a concentration were also determined for two shore locations: station B was located in a small stream which feeds into the northern end of the lagoon, and station TC was located in a rather stagnant body of water near the entrance of a larger stream into the western portion of the lagoon.

RESULTS

The results are summarized in Table 1. Definite trends within the lagoon were quite evident.

Chlorophyll a increased continuously through the channel to the most distant north and west regions of the lagoon (Fig. 1). Chlorophyll a values ran from less than 1 mg/m^3 outside the channel to almost 20 mg/m^3 at the western tip of the lagoon.

Phytoplankton productivity showed a similar trend, ranging from 8.31 mg C fixed/m^3 per hour outside the channel to 145.17 mg C fixed/m^3 per hour at the western corner.

The productivity index (PI), productivity per unit chlorophyll a, essentially a specific growth rate measurement, showed a rather different trend. The highest PI was found outside the lagoon, and values generally decreased to the north and west. An exception to this trend was found at the western corner where the PI reached a relative peak of 8.63 mg C fixed/hr per mg chlorophyll a, a peak concomitant with the highest nutrient concentrations found in the lagoon.

Nutrient concentrations also showed rather clear-cut trends, generally being high outside the channel; decreasing through the channel and northward, but increasing in the western corner. The highest concentrations of both nitrate and phosphate were found in the western loch. Nitrate varied from 0.63 μg-at/liter outside the lagoon to undetectable levels directly inside the channel and increased westward to a maximum concentration of 1.4 μg-at/liter. Phosphate was detectable and relatively abundant at all stations, similar concentrations (0.14 μg-at/liter) being found outside the lagoon, through the channel, and over the northern flats, whereas the western maximum reached 0.33 μg-at/liter. Ammonia showed a somewhat different trend from either nitrate or phosphate, it being highest (0.93 μg-at N/liter) outside the channel, barely detectable throughout most of the lagoon and reaching a relative maximum of 0.12 μg-at N/liter in the western corner. Regrettably, the ammonia method is not as sensitive as those of nitrate and phosphate, and this limits the interpretation that can be made of these data.

Station B, located well inland of the lagoon in a stream running through relatively unpopulated areas, had no detectable ammonia but did have rather large amounts of nitrate and phosphate (0.74 and 2.00 μg-at/liter, respectively). Although recent rainfall had been negligible and many similar streams had completely dried up, this particular stream maintained a rather rapid flow rate and had a small amount of chlorophyll a present.

Circulation in the area of station TC was very restricted. Based on tidal observations, Gallagher (personal communication) estimated the mean residence time of water in the western portion of the lagoon to be about 2 weeks as compared to about 12 hours for water near the entrance channel. Furthermore, the prevailing easterly winds produced a westward surface drift which caused an accumulation of less dense surface water in this area. There were extensive patches of algae floating on the surface, and a marked thermocline was present in less than 1 meter of water. The nutrient concentrations, however, were quite high, and the standing crop of phytoplankton was comparable to that in the far western corner of the lagoon.

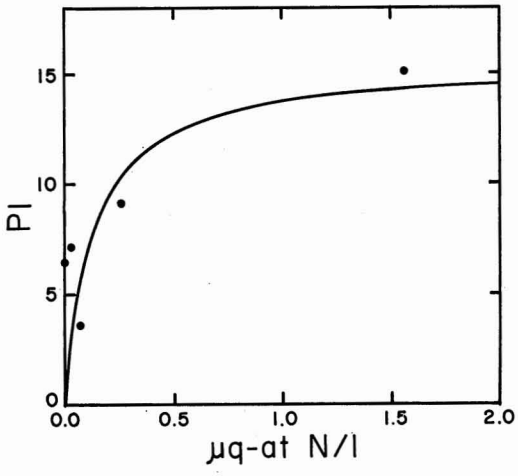

FIG. 2. Productivity Indices as a function of total fixed nitrogen concentrations for the stations in sector 1. K_s = 0.13 µg-at/liter and PI_{max} = 15.6 mg C/mg chl a per hour.

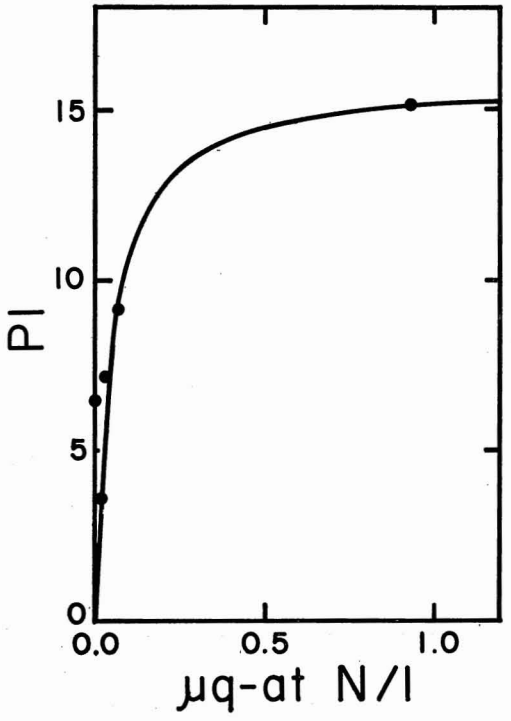

FIG. 3. Productivity Indices as a function of ammonia concentrations for the stations in sector 1. K_s = 0.049 µg-at/liter and PI_{max} = 15.9 mg C/mg chl a per hour.

DISCUSSION

To draw any conclusions from the limited amount of data available we must assume that the phytoplankton population in the lagoon was in steady state with respect to its supply of essential nutrients. The fact that the period immediately preceding the survey was one of low rainfall makes this a tenable assumption.

In a non-nutrient-limiting environment the growth rate of a population is maximal and limited only by its own intrinsic rate of increase under the prevailing conditions of temperature and light. Submaximal growth rates would then reflect nutritional deficiencies in the water mass.

Nutrient-limited growth of phytoplankton has been shown to require a two-step model: the first step utilizes a hyperbola to relate uptake rate to nutrient concentration in the medium; and the second step, directly coupled to the first, utilizes a similar hyperbola to relate growth rate to the intracellular nutrient concentration (Droop, 1968; Caperon, 1968; Caperon and Meyer, 1972*a*). This work has shown that under steady-state conditions a similar hyperbola can be used as a good approximation to describe growth rate directly as a function of environmental nutrient concentration, but the half-saturation constant here is much less than the half-saturation constant for uptake rate. The work of MacIsaac and Dugdale (1969) and Caperon and Meyer (1972*b*) suggests that this kinetic description is applicable to mixed phytoplankton populations adapted to the same nutrient-limited regime. The hyperbola $\mu = \mu_m S/(K_s + S)$, where μ is growth rate, S is substrate concentration and μ_m and K_s are constants, is used to investigate the hypothesis that the stations in sector 1 represented a nutrient-limited regime.

In sector 1 fixed nitrogen was in the nutrient-limited range for phytoplankton adapted to oligotrophic environments (Eppley, Rogers, and McCarthy, 1969). Fig. 2 is a plot of PI as a function of total fixed nitrogen at these stations. The curve is a least squares fit of the data to this hyperbola, with a half-saturation constant, K_s, of 0.13 µg-at/liter and maximum PI, μ_m, of 15.6 mg C/mg chl a per hour. We have assumed that growth rate does not reach zero until the nutrient concentration falls to zero. It has been shown in laboratory experiments

(Caperon and Meyer, 1972*b*) that this is not usually the case for nitrate-limited situations. Growth, or nutrient uptake, stops while there is still some small amount of limiting nutrient in the water. The determination of this intercept requires extremely precise determinations and is best accomplished under controlled laboratory conditions. The assumption of a zero-zero intercept is adequate for our present purposes.

Ammonium is preferentially used over nitrate, so it may be more appropriate to consider only this form of fixed nitrogen. Fig. 3 is a plot of PI as a function of ammonium concentration and the fitted hyperbola has a K_s of 0.049 μg-at/liter and a μ_m of 15.9 mg C/mg chl a/hr.

The half-saturation constants for these two curves compare with 0.13 μg-at/liter for nitrate-limited laboratory populations and 0.02 μg-at/liter for ammonium-limited laboratory populations (Caperon and Meyer, 1972*b*). Unfortunately, the limitations already mentioned regarding the method of ammonia determination preclude too much emphasis being placed on this excellent fit, since all but one of the values are below the lower limits of good reliability of the method.

The source of fixed nitrogen to sector 1 may be either open ocean water or a terrestrial input outside the lagoon. Because the surrounding tropical ocean water is part of the South Equatorial Current System and is one of the most nutrient-poor areas of the Pacific, a more profitable examination of the second alternative is suggested. A nearby open ocean outfall site does in fact exist and the effluent enters the ocean about 1,000 m southwest of the lagoon entrance.

Observations of circulation patterns of the waters immediately adjacent to the lagoon entrance are lacking, but the large tidal exchanges, perhaps aided by nearshore eddy systems, apparently direct a biologically significant portion of this effluent material into the lagoon.

At station 1 we found abundant quantities of fixed nitrogen and near maximal growth rates. Chlorophyll a concentration was 0.55 mg/m^3, substantially lower than that at station 2 inside the reef. However, these stations were measured on a falling tide when a substantial current was flowing out of the channel. During the preliminary fluorometric survey, we measured the chlorophyll a concentration at station 1 on a rising tide and found it to be 0.04 mg/m^3, an order of magnitude less than that measured on the falling tide. Obviously the increased biomass generated in the lagoon was being diluted as it entered the ocean, and the amount of chlorophyll present at station 1 on a falling tide did not represent the amount present in the surrounding open ocean waters. Since no productivity measurements were done on the 1st day, however, we have no comparative estimate of the open ocean PI.

It is difficult to compare a PI_{max} with the μ_m developed for laboratory cultures. This is due both to uncertainty in the interpretation of C^{14} measurements and the artificial environment in laboratory cultures. A PI is converted to a specific growth rate by multiplying by the chlorophyll-to-carbon ratio for the population. This ratio has been shown to vary with steady-state nutrient-limited growth rate (Caperon and Meyer, 1972*a*). Selecting a value of 0.18 mg chl a/mg-at carbon, which is appropriate for a population growing at near-maximum growth rate, converts 15.6 mg C/mg chl a per hour to 0.234 hr^{-1}. If we assume that a short-term measurement of carbon uptake near midday overestimates daily growth rate for the natural day-night cycle at this latitude and time of year by about a factor of 2, we get a μ_m for the C^{14} measurements of 0.117. Note that this value is somewhere between gross and net primary production. It compares with μ_m values of 0.090, 0.087, 0.076, and 0.062 for *Coccochloris stagnina*, *Cyclotella nana*, *Dunaliella tertiolecta*, and *Monochrysis lutheri*, respectively, growing in continuous fluorescent light at 5.8 gm-cal cm^{-2} hr^{-1}. These are net growth rates and should, therefore, be somewhat lower than rates calculated from C^{14} determinations.

In general, one could not hope for better comparison between field and laboratory results for both the μ_m and K_s values. Thus it seems quite apparent that phytoplankton growth in sector 1 of Pala Lagoon was limited by some form of fixed nitrogen. The population at station 1 outside the channel appeared to be approaching maximal attainable growth rates and was likely limited in size by grazing pressure

and physical dilution. Because the water samples were taken on a falling tide, conclusions about growth at this station will not be representative of the surrounding ocean waters.

The growth rate in sector 2 was apparently being controlled by a different mechanism. The data indicate that the nutrient source for sector 1 was outside the lagoon. Fixed nitrogen essentially disappeared in a wide north–south band across the lagoon. The very large concentrations observed in the western corner must then have represented enrichment from runoff and/or sewage waste being added to the lagoon. In light of the abundant fixed nitrogen available in this sector, we may conjecture that the growth rate there was being controlled by some other nutrient species. Although we have no data to substantiate this, it is possible that, in an area such as this with high productivity, high biomass, and abundant macronutrients, a trace metal or other micronutrient may very well be the limiting factor on population growth. Toxic inhibition due to accumulated metabolites cannot be ruled out in this rather stagnant area.

If the growth rates in sectors 1 and 2 are in fact being limited by two different nutrients, then the possibility exists that in a mixture of these two water types either of these two nutrients or perhaps a third could become limiting. Such limitation would depend on the concentration of essential nutrients in each type and the proportions of each type in the mixture. This would create a third rather transient sector at or near the sectors 1 and 2 interface which would shift position and size in response to the amount of stream runoff entering sector 2 and the extent of tidal penetration. This transition area was not detected in the present survey.

During the sampling period the major nutrient input to sector 2 was quite obviously the stream near station TC. Whether this is true in times of high rainfall is unknown. The situation may be quite different when all the streams are running, depending on whether the supply of limiting nutrient to sector 2 is in the runoff water itself or the wastes discharged into the lagoon with it. The data from station B may clarify this somewhat. If we assumed that water from this station was representative of "unpolluted" stream runoff and remained in this state until it entered the lagoon (coliform counts bear this out; P. Bienfang, personal communication), then the growth response of the phytoplankton population in this area to this water would have been an indication of its enrichment value.

The fluorometric survey detected an increase in pigment concentration in this area, but the most northern lagoon station (no. 6) had the lowest PI in the lagoon and was clearly within the nitrogen-limited area. Possibly a productivity station at the extreme northern tip of the lagoon would have found a small area analagous to sector 2, but the very different nutrient characteristics of stations B and TC allow the conclusion that the stimulation observed in the western portion of the lagoon (sector 2) was due to the sewage effluents present in the stream runoff.

CONCLUSIONS

At the time of this study the primary productivity of the phytoplankton population in the greater part of Pala Lagoon was limited by the supply of fixed nitrogen. An extended time series of data under various conditions of rainfall might modify our conclusions but it would seem that the major nutrient inputs are sewage rather than runoff.

If the proposed dredging were to have any effect on the primary productivity, it would be by changing the circulation patterns and flushing rates of the lagoon, and the degree of effect would depend upon the magnitude of these changes. Ignoring any short-term perturbations associated with the dredging operation itself, we affirm that the proposed change in the configuration of the lagoon would have several important results. Assuming our observations to be representative of the general situation, we believe that the sector 1 regime would, with an increase in lagoon-ocean exchange, embrace a larger part of the lagoon, thereby extending the area of higher productivity while lowering the standing crop.

Several changes could be effected in sector 2 if the flushing is substantially improved. Some of the accumulated fixed nitrogen in this area could be utilized in increased production in

sector 1. Ocean water coming into the sector may very well provide some amount of whatever nutrient is limiting in this sector. Whether or not this would be enough to shift this sector to a nitrogen-limited regime is open to question, but here again the standing crop would probably be diluted. The direction of the changes would be to reduce the dissimilarity between sectors 1 and 2. The magnitude of the shift would depend on the magnitude of the changes in circulation and flushing.

Any increase in urbanization in the area will increase the waste load in the lagoon and surrounding open ocean waters. The growth rate stimulation apparent in sector 1 at the present waste discharge level would be increased, and the affected area itself would be enlarged with increased lagoon-ocean exchange. The resulting tendency toward increased standing crop would probably be offset by the higher dilution factor. Thus the subsequent steady state would likely be characterized, at least initially, by higher productivity and a generally lower standing crop in most of the lagoon.

If the proposed dredging decreases the lagoon-ocean water exchange rate as has been suggested (Brent Gallagher, personal communication), these effects would be essentially reversed. Sector 1 would decrease in area and sector 2 would embrace more of the lagoon. A further depression of productivity indices in the extended parts of sector 2 could be expected, but it is likely that chlorophyll a values would increase because of diminished mixing with open ocean water.

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LITERATURE CITED

CAPERON, J. 1968. Population growth response of *Isochrysis galbana* to nitrate variation at limiting concentrations. Ecology 49: 866–872.

CAPERON, J., and J. MEYER. 1972*a*. Nitrogen-limited growth of marine phytoplankton. Part I: Changes in population characteristics with steady state growth rate. Deep-Sea Res. 19: 601–618.

———. 1972*b*. Nitrogen-limited growth of marine phytoplankton. Part II: Uptake kinetics and their role in nutrient limited growth of phytoplankton. Deep-Sea Res. 19: 619–632.

DROOP, M. R. 1968. Vitamin B_{12} and marine ecology. Part 4. J. Mar. Biol. Ass. U.K. 48: 689–733.

EPPLEY, R. W., J. N. ROGERS, and J. J. MCCARTHY. 1969. Half-saturation constants for uptake of nitrate and ammonium by marine phytoplankton. Limnol. Oceanogr. 14: 912–920.

LORENZEN, C. J. 1966. A method for the continuous measurement of *in vivo* chlorophyll concentration. Deep-Sea Res. 13: 223–227.

MACISAAC, J. J., and R. C. DUGDALE. 1969. The kinetics of nitrate and ammonium uptake by natural populations of marine phytoplankton. Deep-Sea Res. 16: 45–57.

SOLORZANO, L. 1969. Determination of ammonia in natural waters by the phenolhypochlorite method. Limnol. Oceanogr. 14: 799–801.

STEEMAN-NIELSEN, E. 1952. The use of radioactive carbon (C^{14}) for measuring organic production in the sea. J. Cons. Int. Explor. Mer 18: 117–140.

STRICKLAND, J. D. H. and T. R. PARSONS. 1968. A practical handbook of seawater analysis. Bull. Fish. Res. Bd. Can. 167.

WOLFE, D. A. and C. L. SCHELSKE. 1967. Liquid scintillation and Geiger counting efficiencies for C^{14} incorporated by marine phytoplankton in productivity measurements. J. Cons. Int. Explor. Mer 31: 31–37.